Diet composition has a greater effect on larval and juvenile polar cod (*Boreogadus saida*) growth rates than temperature in a warming Pacific Arctic

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Abstract

The relative influences of temperature and diet on growth of marine fish are especially relevant in high-latitude ecosystems where warming temperatures and loss of sea ice alter the thermal and feeding environment for cold-adapted species. Larval and juvenile fish may be particularly vulnerable to warming since access to favorable habitats in the spring and summer is necessary for growth and overwinter survival. Therefore, we focused on three warm, low-ice years (2017-2019) in the Chukchi Sea and on a nodal forage fish species in Arctic food webs (polar cod: *Boreogadus saida*) to better understand the influences of warming temperatures and diet on growth during the first year of life. Paired diet data from gut content analysis and daily otolith-derived growth rates indicated that diet had a greater impact on growth than temperature. Generalized additive models that included diet information explained a large portion of variability in recent growth [5-d average preceding capture; coefficient of determination (R^2) 0.43-0.45] compared to those that excluded diet but incorporated temperature and salinity (R^2=0.06-0.07) and a year effect (R^2=0.20-0.30). Relationships between diet and growth suggest that polar cod fed on a range of taxa during warm years but benefited from access to remnant sea-ice associated prey such as *Calanus glacialis* copepods. Larval and juvenile polar cod may be resilient to warming temperatures if preferential high-quality prey persists into the summer, but sea-ice retreat and inundation of subarctic zooplankton earlier in the year could have detrimental impacts on polar cod growth and survival.

1. Introduction

Fast growth and large body size are often associated with increased survival of marine fish during the first year of life due to lower risk of predation and presumed higher body condition (Heintz and Vollenweider, 2010; Robert et al., 2023; Sogard, 1997). Growth variation during the early life stages is largely driven by a combination of temperature (Atkinson, 1994) and food availability to meet metabolic demands (Mazur et al., 2007; Sreenivasan and Heintz, 2016). Under this paradigm, environmental change or small-scale variation in local conditions may have direct or indirect effects on growth and survival.

High-latitude ecosystems are undergoing rapid environmental change where warming water temperatures and changes in primary and secondary productivity affect the thermal and

feeding environment for the early life stages of marine fish (Kimmel et al., 2023; Leu et al., 2011; Søreide et al., 2010). In the Arctic, earlier summer sea-ice retreat alters the composition of basal resources from largely sea-ice algae to a greater contribution from subarctic primary producers (Lee et al., 2019). Loss of sea ice also leads to lower abundance of large lipid-rich copepods such as *Calanus glacialis* that are important prey for larval and juvenile fish (Bouchard and Fortier, 2020; Spear et al., 2020; Strasburger et al., 2014). For polar cod [*Boreogadus saida* (Lepechin, 1774); Gadidae; alternatively referred to as "Arctic cod"], the most abundant forage fish in the Arctic (Geoffroy et al., 2016; Kono et al., 2016; Welch et al., 1992), warmer temperatures and decreases in *C. glacialis* could affect growth by exposing fish to temperatures above their thermal optimum (Laurel et al., 2016) and limiting preferred prey (Bouchard and Fortier, 2020).

Polar cod serve as a link between sea-ice algal primary producers and higher trophic levels such as seals, whales, and sea birds (Hop and Gjøsæter, 2013; Kohlbach et al., 2017), which merits a better understanding of the impacts of warming and diet shifts on growth and survival of this nodal species (Mueter et al., 2016; Welch et al., 1992). Polar cod life history is closely tied to sympagic ecosystems such that large-scale loss of sea-ice habitats may lead to overall declines in abundance and biomass (Geoffrey et al., 2023) or restrict polar cod distributions due to borealization of their southern range margin (Axler et al., 2023; Levine et al., 2023; Randall et al., 2019; Spear et al., 2020). Laboratory studies highlight the potential nuanced interaction between warming and growth due to metabolic constraints, whereby polar cod larval growth rates increase with temperature up to ~5°C-7°C, although mortality also increases (Koenker et al., 2018). In the natural environment, extensive declines in sea ice and warming temperatures will likely increase metabolic demands for larval and juvenile polar cod (David et al., 2022) while simultaneously reducing access to favorable large, lipid rich copepod prey that rely on sea-ice algal productivity (Bouchard and Fourtier, 2020; Søreide et al., 2010). There is evidence to suggest benefits of early ice break-up and early hatch to extend the growing season (Bouchard et al., 2017), but warmer temperatures are generally associated with reduced body size and condition of juveniles, with consequences to pre-winter provisioning and overwinter survival (Copeman et al., 2017; 2022b). Despite overarching detrimental effects of loss of sea ice on polar cod, variation in spatial distributions, diet resources, hatch timing, and growth suggest

that the species may be adaptable, or have complex responses, to warming (Bouchard and Fortier, 2011; Bouchard et al., 2017; Goldstein et al., 2023; Levine et al., 2023).

Few empirical studies have addressed the combined influences of temperature and diet on polar cod growth and size during the early life stages, particularly in the Chukchi Sea that serves as a Pacific "gateway" to the Arctic (David et al., 2022; Geoffroy et al., 2023). There are even fewer studies in the Chukchi Sea continental shelf ecosystem addressing the influence of environmental conditions on individual larval and juvenile polar cod growth (Chapman et al., 2023) despite the prevalence of age-0 polar cod on the productive shelf, and their important trophic role in Arctic food webs (Levine et al., 2023). To help fill this gap in understanding about polar cod vulnerabilities to a changing Arctic, we use otolith-derived growth rates and morphological diet data from larval and juvenile fish collected in the Chukchi Sea. We focus on three study years (2017-2019) that provide possible representations of a "future" Arctic with reduced sea ice, warm temperatures, and an inundation of subarctic water masses (Goldstein et al., 2023; Levine et al., 2023; Spear et al., 2020) to determine the influences of temperature and diet composition on growth and body size of polar cod during the early life stages. Warm temperatures combined with reduced access to high quality prey could lead to predominantly negative relationships between temperature and growth for cold-adapted polar cod. We hypothesize that during the three warm study years, polar growth rates will be suppressed at the highest observed temperatures, and that potential positive relationships between temperature and growth at moderately warm temperatures (Koenker et al., 2018) will be mediated by access to ice-associated high-quality prey.

2. Methods

2.1 Survey data and specimen collection

Oceanographic data and polar cod samples were collected aboard surveys conducted in the late summer months (August-September) of 2017, 2018, and 2019 (Supplemental Table 1) in the Chukchi Sea (Figure 1). Vertical profiles of temperature and salinity were measured using Sea-Bird Electronics (SBE) 911plus conductivity, temperature, depth recorders (CTD) just prior to or immediately after net tows or a SBE 49 FastCAT CTD affixed to ichthyoplankton nets. CTD data were processed using SBE software with values averaged in 1 m depth bins. Fish were

collected using paired 60-cm (505 µm mesh) and 20-cm (153 µm mesh) bongo nets that were towed obliquely from the surface to 10 m off the bottom or a maximum depth of 200 m (Matarese et al., 2003). All fish samples were sorted from one side of each paired net to preserve the other side for quantitative catch data. To increase sample sizes in 2018, larval and juvenile specimens [n=3; < 35 mm standard length; (Vestfals et al., 2021)] were opportunistically collected using a Methot frame trawl (2.23 m by 2.23 m square-frame opening, 2 mm hexagonal mesh, and 500 µm codend mesh; Methot, 1986). The Methot trawl was towed for 8 to 21 minutes, targeting the pelagic scattering layer or the chlorophyll maximum. Samples were stored at -80°C. Thawed fish were measured in the laboratory (standard length, mm). Stomachs were removed and placed in 70% ethanol to prevent degradation.

2.2 Otolith-derived age and growth data

Lapillar and sagittal otoliths were extracted for daily age estimation since lapillus daily increment formation has been confirmed for polar cod (Bouchard and Fortier, 2011) but sagittae are often used for daily age estimation of gadids due to interpretability (Almeida et al., 2024; Dougherty, 2008). Lapilli were mounted in Crystalbond™ 509 thermoplastic cement with no other preparation. Sagittae were transverse thin sectioned by mounting otoliths in Crystalbond™ 509 and manually polishing with fine grit lapping film (ÅngströmLap®; 3 µm) followed by a buffing cloth and 0.05 µm Buehler MasterPrep polishing suspension. Lapilli and sagittae were aged using a compound microscope and a 100× oil immersion objective. Otoliths were aged blindly (no knowledge of fish length or prior age estimates) by a single reader by imaging otoliths (focused on the primordium) and annotating otolith daily increments using ImagePro 10 software (Media Cybernetics). A new image was obtained for each age estimate, with a minimum of two age estimates for each fish. A specimen was retained for analyses if the coefficient of variation among all age estimates was <10%. Final ages were averaged and rounded to integer age. Otoliths were aged from a total of 83 fish, and 72 specimens met the agreement criteria for inclusion in analyses (Supplemental Table 1). Comparisons of fish daily age estimates obtained from sagittae and lapilli (n=68 fish) showed good agreement, supporting the use of either otolith for age determination [ordinary least squares regression (OLS): $Age_{lapillus} \sim 0.97 * Age_{sagitta} + 1.86$; $R^2=0.97$, $p < 0.001$].

The assumption that daily otolith increment widths are correlated with somatic growth rates (Campana 1992; Sponaugle 2009) of polar cod was supported by a correlation between lapilli radii [longest growth axis (posterior)] and fish lengths measured from a random subset of specimens (n=47; OLS: otolith radius=1.32 * daily age + 12.58; R^2=0.82, $p < 0.001$). Lapillus increment widths were measured along the posterior growth axis to estimate growth rates from three time periods during the early life history of each fish: (1) Recent growth was defined as daily increment widths averaged across the most recent 5 full days of growth prior to capture (excludes the partial increment on the day of capture; μm/d). (2) Past growth was defined as average daily increment widths on the preceding 6-10 days before capture (μm/d). (3) Early growth was measured as the lapillus otolith radius from the primordium to day 10 post-hatch (e.g., μm/10d; images were focused on the primordium). Growth preceding capture (recent and past growth) were estimated from lapillus images focused on the edge of each otolith to ensure a comparable focal plane among all specimens. For these measurements, a transect was drawn from the otolith edge to the primordium along the growth axis and daily increment widths were measured (starting from the otolith edge) until increments were difficult to discern due to the focal plane. This resulted in differences in the total number of days before capture measured for each specimen. However, all specimens but two included measurements for the most recent 10 days preceding capture.

2.3 Diet data and analyses

Morphological diet data were obtained by removing the alimentary canal from each fish and using minutien pins to separate zooplankton prey in glycerol (Llopiz and Cowen, 2009). Prey were identified to the lowest taxonomic level possible and enumerated using a stereomicroscope with a camera and ImagePro 10 software. Copepodite and adult copepods were not differentiated due to digestion, and some prey taxa were grouped at a higher taxonomic level for simplification of analysis. Diet data (raw data as numerical counts of each taxonomic group) were visualized and simplified with Principal Components Analysis (PCA) using taxa whose counts comprised at least 1% of the total observations among all taxa. A Hellinger transformation (square root of relative abundance) was conducted on the diet count data prior to the PCA to address spurious similarities among specimens due to shared absence of species in diet data (double-zero problem; Legendre and Gallagher, 2001; Legendre and Legendre, 2012).

To better link changes in diet with potential declines in sea ice and warming temperatures, we extended work presented in Goldstein et al. (2023; see Methods section for detailed description of methods and analyses) to compare gut content diet data with available $\delta^{13}C$ compound-specific stable isotope analysis of amino acid (CSIA-AA) data from homogenized polar cod tissues (excluding heads and stomachs) for a subset of fish from 2017 and 2018. The goal of this analysis was to better understand whether changes in diet were associated with changes in food web basal carbon resources such as sea-ice-algal derived carbon or pelagic phytoplankton. Broadly, CSIA-AA values from essential amino acids exhibit minimal or no trophic fractionation such that CSIA-AA fingerprints (row-centered CSIA-AA for each specimen or observation) mirror CSIA-AA fingerprints from carbon sources (Larsen et al., 2013). Potential carbon sources considered for this analysis were sea-ice algae (iPOM; determined from ice-associated particulate organic matter), pelagic primary producers (pPOM; determined from pelagic particulate organic matter), microalgae, *Synecchococcus* spp. and dinoflagellates [typically subarctic taxa; (Flombaum et al., 2013)], and bacteria. We present a Linear Discriminant Analysis adapted from Goldstein et al. (2023) to visualize previously established relationships between CSIA-AA fingerprints from carbon sources and polar cod samples. Additional details that are specific to this study are available in Goldstein et al. (2023). We then used a multivariate redundancy analysis (RDA) with Euclidean distance to determine whether changes in diet corresponded with changes in basal carbon resources for polar cod. RDA is a constrained ordination method where ordination vectors of response variables are linear combinations of the predictor variables (Legendre and Legendre, 2012). Here, we incorporated PCA axis 1, PCA axis 2, and PCA axis 3 scores from gut content analyses as predictor variables. Response variables were row-centered CSIA-AA fingerprints for Isoleucine (Ile), Leucine (Leu), and Valine (Val) from polar cod samples. Other amino acids were excluded from the analyses due to multicollinearity (variance inflation factors: VIFs >3).

2.4 Influence of environment and diet on otolith-derived growth

Analysis of Variance (ANOVA) followed by Tukey's Honestly Significant Difference (Tukey) post-hoc tests were used to determine whether there were average differences in early growth, past growth, recent growth, and diet PCA axis 1 scores (since axis 1 encompasses the most variability in the data) among years. ANOVA tests using a significance threshold of $p <$

0.05 were conducted after confirming that growth metrics were not correlated with age and confirmation that data followed a normal distribution and exhibited homogeneity of variance (Sokal and Rohlf, 1995).

Generalized additive models (GAMs; Gaussian distribution and "identity" link function) were then used to test for potential drivers of variation in growth. Specifically, GAMs focused on the influence of intrinsic (i.e., age and early growth) and extrinsic (i.e., temperature, salinity, diet) factors on growth rates. Since diet and *in situ* data only represent recent conditions, the focal GAM response variable was recent growth (5 days preceding to capture). A second set of models was also tested with past growth (6-10 days preceding to capture) to determine if conditions at capture were correlated with longer-term patterns in growth. For each response variable, two sets of models were tested to focus on the influences of intrinsic factors, environmental conditions, and diet on growth (Equation 1) or the influences of only intrinsic factors and environmental conditions on growth (Equation 2).

Equation 1: $\text{Growth} = s(S_{200}) + s(T_{20}) + s(S_{20}) + s(\text{Age}) + s(\text{Growth}_{\text{early}}) + s(\text{PC1}_{\text{diet}}) + s(\text{PC2}_{\text{diet}}) + s(\text{PC3}_{\text{diet}})$

Equation 2: $\text{Growth} = s(T_{200}) + s(S_{200}) + s(T_{20}) + s(S_{20}) + s(\text{Age}) + s(\text{Growth}_{\text{early}})$

Here, s() refers to smooth terms with a thin plate spline basis and knots set to 4 to avoid overfitting. The response variable, Growth, is recent growth or past growth determined from otolith increment widths (µm/day). T_{200} and S_{200} are temperature (°C) and salinity (PSU), respectively, averaged over the top 200 m of the water column which represented the entire water column at many of the stations (Fig. 1) and encompasses the entire depth range of the bongo net tows where fish were collected. T_{20} and S_{20} are surface temperature and salinity, respectively, averaged over the top 20 m of the water column. The Chukchi Sea water column in the summer months is often stratified with a typical surface mixed layer depth of ~20 m (Weingartner et al., 2013). Water mass composition evolves throughout the season (Lin et al., 2019). However, surface waters are generally comprised of cool low salinity sea-ice melt water and warmer Alaskan coastal (Pacific-origin) water masses, whereas deeper depths are composed of higher-density waters such as Bering Sea waters and winter waters (Weingartner et al., 2013), a pattern also observed during late summer in warm years (Goldstein et al., 2023). A depth of 20 m was selected since polar cod larvae primarily reside in surface waters (Geoffroy et al., 2023)

and because this depth approximates conditions in the surface mixed layer, where sea-ice melt water and ice-associated taxa might reside. Age is fish daily age. $Growth_{early}$ is otolith radius (μm) from the first 10 days of life and was included to address potential carryover effects of early life growth rates on recent growth. $PC1_{diet}$, $PC2_{diet}$, and $PC3_{diet}$ are PCA axis 1, 2, and 3 scores from the diet PCA analysis and represent a measure of diet resemblance among specimens. Variables included in the full models are those with VIFs < 3, resulting in the exclusion of T_{200} from Equation 1 due to collinearity with T_{20}. We elected to include T_{20} as a variable in the model rather than T_{200} since it was retained in the recent growth model using Equation 2, facilitating comparisons among models with and without diet data (see Table 1 and Results).

We also tested several models that addressed potential year effects to confirm that associations between growth, environmental variability, and diet were not linked with other processes that varied among years. (1) We tested the selected model from Equation 1 excluding the year 2019 since diet differed in that year (see Results). (2) We tested the selected model from Equation 2 using only the subset of samples with diet data to facilitate more direct comparisons among models with and without diet information. (3) We compared models (Equation 1 and Equation 2) that included year as a fixed effect as well as a simple random effect (intercept; Pedersen et al., 2019) since other processes such at maternal effects, selective predation, or competition could vary by year and affect growth (Berkeley et al., 2004; Fortier and Harris, 1989; Sogard, 1997). Three years of data are fewer than the recommended group levels (5-6) for random effects (Bolker et al., 2009), but evidence suggests that there is little risk to testing models with fewer than five groups (Gelman and Hill, 2007; Gomes 2002; Oberpriller et al., 2022). For models that excluded diet data (Equation 2), the random or fixed effect of year could encompass interannual variability in diet as well as other processes (e.g. diet is an "unmeasured' variable in these models). Therefore, if an effect of year improved models that lacked diet data, then we conducted model selection on a set of models with and without a year effect to better disentangle the influence of "year" compared to temperature, salinity, age, and early growth.

GAMs were fit using restricted maximum likelihood estimation and models were compared using Akaike Information Criterion adjusted for small sample sizes (AICc; Akaike, 1998). If AICc differed by ≤2 then the more parsimonious model was selected. For each model

formulation, a stepwise variable selection procedure was conducted and final models were selected among the most supported candidate models (Burnham and Anderson, 2002; Zuur et al., 2009). For all models, smooth terms were replaced with a linear relationship if the estimated degrees of freedom (edf) were equal to 1. All data analysis was conducted in R (R Core Team, 2024) using packages FSA for age analyses (Ogle et al., 2025), Vegan (Oksanen et al., 2025) and MASS (Venables and Ripley, 2002) for multivariate analyses, and mgcv for GAMs (Wood, 2017).

3. Results

Spatial extent and coverage of surveys differed among the study years, but polar cod catch locations in late summer were primarily in the northeast region of the Chukchi Sea in cooler water temperatures (Fig. 1, Supplemental Table 1, Supplemental Fig. 1). Hatch dates were similar in 2017 and 2019, and later in 2018 when temperatures were also generally cooler at catch locations (Figs. 1, 2A). Fish size-at-age overlapped among years, but fish were slightly larger in 2019 (Fig. 2B). Early growth [Fig. 2C; ANOVA: $F(2, 69) = 4.99$, $p < 0.01$; Tukey: 2017 = 2018, 2018 = 2019, 2017 < 2019], past growth [Fig. 2D; ANOVA: $F(2, 67) = 20.00$, $p < 0.001$; Tukey: 2017 = 2018, 2017 & 2018 < 2019], and recent growth [Fig. 2D; ANOVA: $F(2, 69) = 9.67$, $p < 0.001$; Tukey: 2017 = 2018, 2017 & 2018 < 2019] were greatest in 2019. Trends in growth rates indicated elevated past growth compared to recent growth in 2019 (Fig. 2D). Growth rates were relatively similar across overlapping ages in 2017 and 2018 (Fig. 2E). Fish in 2019 consistently grew faster, though there was a narrower range in overlapping ages between 2019 and the other years (Fig. 2E). There were no clear spatial patterns in recent growth (Fig. 1, Supplemental Fig. 2).

Polar cod diets in 2019 were distinct from the other years (Fig. 3) as confirmed by significant differences between PC axis 1 scores [ANOVA: $F(2, 48) = 13.5$, $p < 0.001$; Tukey: 2017 = 2018, 2017 & 2018 < 2019]. This overarching variation in diet was likely minimally related to body size (diet ontogeny) or *in situ* water temperature (Fig. 3). Positive scores along PCA axis 1, where all 2019 polar cod diets ordinated, were primarily associated with the presence of the large copepod *C. glacialis* and the smaller copepods, *Oithona* spp. and *Pseudocalanus* spp. as well the absence of unidentifiable copepods (C_UNID). There was divergence along PCA axis 2 among the 2019 fish with a separation between those that primarily

consumed *C. glacialis*, and those that consumed smaller copepod taxa. PCA axis 3 captured similar patterns to PCA axis 1, but with negative scores reflecting consumption of small calanoid copepods (C_Cal_sm) and positive scores reflecting greater consumption of *C. glacialis*, *Oithona* spp., and unidentifiable copepods (Fig. 3D). PCA axis 4 explained a small proportion of variability in the data (7.72%) but primarily separated consumption of the broad taxonomic grouping of large calanoid copepods from *C. glacialis*, *Pseudocalanus* spp., and unidentified copepods. Individual fish diets varied to a greater degree in 2017 and 2018 than 2019, but some fish diets resembled those from 2019 (Fig. 3A, C).

Diet resources determined from CSIA-AA were similar in 2017 and 2018 (Fig. 4A). CSIA-AA data were not available for 2019, potentially affecting observed variation in diet resources and resulting in weak relationships between CSIA-AA and gut contents (Fig. 4B). Only a small proportion of variation in diet data was correlated with changes in CSIA-AA (32.3% based on both constrained axes); nevertheless, there were indications of potential links between diet and basal resources. CSIA-AA values for polar cod primarily overlapped with microalgae and pPOM (Fig. 4A). However, positive PCA axis 1 scores were associated with *Pseudocalanus* spp., which can include temperate and sea-ice associated species in the Chukchi Sea, as well as *C. glacialis* which is a cold-water, ice-associated copepod (Questel et al. 2016; Spear et al. 2020). These positive PCA axis 1 scores were strongly correlated with the amino acid Isoleucine and had a weak negative association with Leucine (Fig. 4). This separation between Isoleucine and Leucine was a major discriminating pattern in the CSIA-AA "fingerprint" for iPOM, which is indicative of carbon resources originating from sea-ice algae, to a greater degree than pPOM which is representative of pelagic primary producers (Fig. 4A).

Recent growth was primarily associated with variation in diet, with only weak relationships with temperature, salinity, or early growth based on comparisons of GAMs that included or excluded diet information (Table 1; Supplemental Table 3). As expected, given few group levels, models with year as a fixed or random effect showed similar results (Supplemental Tables 3 and 4; Gelman and Hill, 2007). There was little support for the inclusion of year as a random or fixed effect in the recent growth diet models (Supplemental Table 3), suggesting that accounting for unmeasured variation among years did not improve model fits. Models without diet information improved when a year effect was included, but all model formulations

corroborated the minimal influences of temperature, salinity, and early growth on recent growth (Table 1; Supplemental Table 3). The substantial impact of diet on recent growth was confirmed by several model comparisons. (1) Since diet information was not available for all samples (Supplemental Table 1), we tested "no diet" models using the identical subset of samples used in "diet" models (n=51) to facilitate comparisons between "diet" and "no diet" model results (Table 1 and Supplemental Table 3). This more direct comparison confirmed that models that included diet information showed considerable improvements over those that excluded diet data. This was especially pronounced when year was not included in the "no diet" model (Table 1), but continued to hold true when "no diet" models included a fixed or random effect of year (Supplemental Table 3; for example see Diet (Eq 1) and No diet (Eq 2) + $Year_{re}$: diet fish only). Since diet differed among years (e.g. 2019), this comparison also suggests that diet affected recent growth to a greater degree, or in addition to, other factors that varied among years. (2) A model that excluded data from 2019 continued to show a substantial impact of diet on recent growth. This ensured that variation in diet in 2019 compared to the other years was not driving the correlations between diet and growth (Table 1).

Recent growth had little to no relationship with age such that age was not included in the final GAMs (Table 1, Supplemental Table 3). Neither temperature nor salinity were retained in the selected recent growth diet model, nor the "no diet" models that included fixed or random effects of year (Table 1; Supplemental Table 3). Early growth was retained in the selected models that excluded diet data, but the relationship was weakly negative, suggesting that early larval growth may have a nominal carryover effect on later growth rates (Supplemental Table 3). Positive PCA axis 1 (primarily greater consumption of *C. glacialis*, *Pseudocalanus* spp., and of *Oithona* spp. and reduced consumption of unidentified copepods) and PCA axis 3 scores (also associated with greater consumption of *C. glacialis* and *Oithona* spp., as well as reduced consumption of small calanoid copepods) were associated with faster recent growth (Table 1; Fig. 5A, B). Relationships between recent growth and hatch dates within each year did not show shifts in growth patterns over the capture season or across ages as would be expected if variation in growth was due to selective mortality (Supplemental Figs. 2 and 3).

Inconsistent relationships between past and recent growth among years, including a relatively flat relationship in 2019, support the supposition that recent growth was primarily

linked with recent feeding rather than a carryover effect of prior condition and growth (Supplemental Fig. 4). Past growth was minimally correlated with temperature and salinity (Supplemental Table 4). Unlike recent growth, all past growth models that included a year effect outperformed those that did not account for year, regardless of whether diet information was incorporated in the models (Supplemental Table 4). The strong relationship between sampling year and past growth suggests that other processes that varied among years had a considerable impact on past growth. These results indicate that diet at capture explained appreciably less variation in past growth than recent growth, in accordance with the expectation that gut contents reflect recent conditions since evacuation occurs on the order of hours to days depending on feeding, temperature, and development (Canino and Bailey, 1995; Hop and Tonn, 1998; Table 1, Supplemental Tables 3 and 4).

4. Discussion

The relative influences of temperature and diet on growth of marine fish is a fundamental ecological question that continues to gain importance in polar regions as sea ice declines and ocean temperatures increase, potentially leading to shifts in phenology, growth rates, and predator-prey mismatch (Atkinson, 1994; David et al., 2022; Geoffroy et al., 2023; Mazur et al., 2007; Meekan et al., 2003). A warming Arctic will likely exacerbate metabolic constraints on growth of cold-adapted species through the combined effects of thermal tolerances and food quality and availability. The relationship between polar cod growth and temperature was weak despite evidence of thermal optima in laboratory experiments (Koenker et al., 2018; Laurel et al., 2016), the potential for interactions between temperature and prey quality, and expectations that reduced sea-ice cover and warming temperatures may limit access to favorable environments (Geoffrey et al., 2023). While lagged effects on growth could differ between temperature and diet, our results suggest that diet had a greater influence on larval and juvenile growth rates than temperature during the three warm study years, largely driven by the consumption of lipid-rich copepods such as *C. glacialis*. These findings suggest that in a warm Arctic, the presence of high-quality prey can support fast growth of larval and juvenile polar cod and buffer against potential negative effects of sea-ice decline.

373 Variation in diet and growth within and among years suggests that access to habitat
374 patches with cooler temperatures and high-quality prey is essential to the adaptability of polar
375 cod to a warming climate. Even during warm years, polar cod were primarily collected in colder
376 water temperatures and at high latitudes (e.g., ~71°N or higher), suggesting differentiation in
377 habitat use that has also been observed for older age-0 fish during colder years in the Chukchi
378 Sea (Marsh et al., 2020). While 2019 was ostensibly the warmest year of the study (Stabeno et
379 al., 2023), polar cod had faster growth and consumed higher quality prey species that are
380 typically associated with Arctic water masses and sea ice. This dichotomy suggests that fish were
381 accessing, or co-occurring with, patches of favorable prey in 2019 despite warm temperatures.
382 During 2017 and 2018, there was greater variation in diet among individuals compared to 2019,
383 yet fish in favorable habitats with high-quality prey grew faster regardless of the year. This
384 pattern suggests that overall slower growth in 2017 and 2018 was driven by variation in feeding
385 habitat, whereby a greater majority of the sampled fish encountered poorer habitats in 2017 and
386 2018 than in 2019. Juvenile polar cod also had low body condition in 2017, but high body
387 condition in 2019 that was comparable to favorable cold years and attributed to localized
388 conditions (Copeman et al., 2022a). These contrasting warm years suggest that annual variation
389 in climate may be mediated by localized processes and highlight the importance of remaining, or
390 remnant, sea-ice habitats and associated prey to support polar cod growth and survival in a
391 "future" Arctic.

392 CSIA-AA results supported the link between favorable diets and lingering sea-ice
393 productivity to support fast growth. CSIA-AA $\delta^{13}C$ from fish tissue reflects basal carbon
394 resources that are influenced by prey consumption and interim trophic linkages. For example,
395 polar cod prey such as *C. glacialis* utilizes a substantial portion of carbon from sea-ice
396 environments (Kohlbach et al., 2016). However, they consume a variety of prey such as
397 microzooplankton, phytoplankton, and sea-ice algae (Campbell et al., 2009; Sherr et al., 2009;
398 Søreide et al., 2010), and reliance on sympagic carbon resources can shift seasonally for *Calanus*
399 species in Arctic food webs (Kohlbach et al., 2024). In warming temperatures, polar cod and
400 their prey may both exhibit diet shifts away from sea-ice resources. Nonetheless, correlations
401 between favorable diets and sea-ice carbon resources were positive, despite lacking data from
402 2019 when diets diverged from other years and relationships between diet and growth were most
403 prominent. This evidence for lingering sea-ice basal carbon resources in polar cod diets further

supports the important role of sea-ice productivity across trophic levels and alludes to the continuing importance of sea-ice carbon resources in Arctic food webs during late summer in warm years.

This study was limited to only warm years in the Chukchi Sea and relatively small sample sizes, necessitating future efforts to contrast the influences of diet and temperature on larval and juvenile polar cod growth across broader environmental and geographic domains. However, the Chukchi Sea ecosystem represents a productive shallow shelf environment that functions as a transitional zone between subarctic and Arctic habitats. As a result, this region is changing at a rapid pace and may provide insight into potential consequences of continuing Arctic sea-ice recession. Comparisons among the study years indicate conditions that promote growth and survival of polar cod in a warming Arctic. For example, reduced sea-ice cover combined with wind reversals in 2017 (Goldstein et al., 2023) potentially impacted distributions of polar cod and their prey, and limited access to ice-associated habitats. This contrasts with 2019 when winds were more consistent, and water masses and temperature showed stronger latitudinal gradients (Levine et al., 2023), potentially supporting remnant sea-ice habitats at higher latitudes despite low ice extent. Notably, variation in diet was strongly correlated with recent growth but less tightly coupled to growth beyond 5-d prior to capture, suggesting that encounters with suitable habitat and high-quality prey could have an expeditious effect on larval and juvenile polar cod growth. The capacity for polar cod to exploit available favorable environments in exceptionally warm years points to adaptability and resilience of the species, but suggests that loss of sea-ice habitats earlier in the warm season and diminished access to high-quality prey have detrimental effects on growth of an important Arctic forage fish species.

Data statement

Data will be made available on request.

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References

Akaike, H., 1998. Information Theory and an Extension of the Maximum Likelihood Principle. In: Parzen, E., Tanabe, K., Kitagawa, G. (Eds.), Selected Papers of Hirotugu Akaike, Springer Series in Statistics. Springer, New York, NY, pp. 199–213. https://doi.org/10.1007/978-1-4612-1694-0_15

Almeida, L.Z., Laurel, B.J., Thalmann, H.L., Miller, J.A., 2024. Warmer, earlier, faster: Cumulative effects of Gulf of Alaska heatwaves on the early life history of Pacific cod.

458 Elementa: Science of the Anthropocene 12, 00050.
459 https://doi.org/10.1525/elementa.2023.00050
460 Atkinson, D., 1994. Temperature and organism size—a biological law for ectotherms? Advances
461 in Ecological Research 25, 1–58.
462 Axler, K.E., Goldstein, E.D., Nielsen, J.M., Deary, A.L., Duffy-Anderson, J.T., 2023. Shifts in
463 the composition and distribution of Pacific Arctic larval fish assemblages in response to
464 rapid ecosystem change. Global Change Biology 29, 4212–4233.
465 https://doi.org/10.1111/gcb.16721
466 Berkeley, S.A., Chapman, C., Sogard, S.M., 2004. Maternal age as a determinant of larval
467 growth and survival in a marine fish, *Sebastes melanops*. Ecology 85, 1258–1264.
468 Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., White,
469 J.-S.S., 2009. Generalized linear mixed models: a practical guide for ecology and
470 evolution. Trends in Ecology & Evolution 24, 127–135.
471 https://doi.org/10.1016/j.tree.2008.10.008
472 Bouchard, C., Fortier, L., 2020. The importance of *Calanus glacialis* for the feeding success of
473 young polar cod: a circumpolar synthesis. Polar Biology 43, 1095-1107.
474 https://doi.org/10.1007/s00300-020-02643-0
475 Bouchard, C., Fortier, L., 2011. Circum-arctic comparison of the hatching season of polar cod
476 *Boreogadus saida*: A test of the freshwater winter refuge hypothesis. Progress in
477 Oceanography 90, 105–116. https://doi.org/10.1016/j.pocean.2011.02.008
478 Bouchard, C., Geoffroy, M., LeBlanc, M., Majewski, A., Gauthier, S., Walkusz, W., Reist, J.D.,
479 Fortier, L., 2017. Climate warming enhances polar cod recruitment, at least transiently.
480 Progress in Oceanography 156, 121–129. https://doi.org/10.1016/j.pocean.2017.06.008
481 Burnham, K.P., Anderson, D.R. (Eds.), 2004. Model Selection and Multimodel Inference.
482 Springer, New York, NY. https://doi.org/10.1007/b97636
483 Canino, M.F., Bailey, K.M., 1995. Gut evacuation of walleye pollock larvae in response to
484 feeding conditions. Journal of Fish Biology 46, 389–403. https://doi.org/10.1111/j.1095-
485 8649.1995.tb05979.x
486 Campana, S.E. 1992. Measurement and interpretation of the microstructure of fish otoliths, pp.
487 59-71. In Stevenson, D.K., Campana, S.E. (Ed.), Otolith microstructure examination and
488 analysis. Canadian Special Publication of Fisheries and Aquatic Sciences 117.

Campbell, R.G., Sherr, E.B., Ashjian, C.J., Plourde, S., Sherr, B.F., Hill, V., Stockwell, D.A., 2009. Mesozooplankton prey preference and grazing impact in the western Arctic Ocean. Deep Sea Research Part II: Topical Studies in Oceanography 56, 1274–1289. https://doi.org/10.1016/j.dsr2.2008.10.027

Chapman, Z.M., Mueter, F.J., Norcross, B.L., Oxman, D.S., 2023. Arctic cod (*Boreogadus saida*) hatching season and growth rates in the Bering, Chukchi and Beaufort seas. Deep Sea Research Part II: Topical Studies in Oceanography 207, 105226. https://doi.org/10.1016/j.dsr2.2022.105226

Copeman, L., Laurel, B., Spencer, M., Sremba, A., 2017. Temperature impacts on lipid allocation among juvenile gadid species at the Pacific Arctic-Boreal interface: an experimental laboratory approach. Marine Ecology Progress Series 566, 183–198. https://doi.org/10.3354/meps12040

Copeman, L.A., Salant, C.D., Stowell, M.A., Spencer, M.L., Kimmel, D.G., Pinchuk, A.I., Laurel, B.J., 2022a. Annual and spatial variation in the condition and lipid storage of juvenile Chukchi Sea gadids during a recent period of environmental warming (2012 to 2019). Deep Sea Research Part II: Topical Studies in Oceanography 205, 105180. https://doi.org/10.1016/j.dsr2.2022.105180

Copeman, L.A., Stowell, M.A., Salant, C.D., Ottmar, M.L., Spencer, M.L., Iseri, P.J., Laurel, B.J., 2022b. The role of temperature on overwinter survival, condition metrics and lipid loss in juvenile polar cod (*Boreogadus saida*): A laboratory experiment. Deep Sea Research Part II: Topical Studies in Oceanography 205, 105177. https://doi.org/10.1016/j.dsr2.2022.105177

David, C.L., Ji, R., Bouchard, C., Hop, H., Hutchings, J.A., 2022. The interactive effects of temperature and food consumption on growth of larval Arctic cod (*Boreogadus saida*): A bioenergetic model. Elementa: Science of the Anthropocene 10, 00045. https://doi.org/10.1525/elementa.2021.00045

Dougherty, A.B., 2008. Daily and sub-daily otolith increments of larval and juvenile walleye pollock, *Theragra chalcogramma* (Pallas), as validated by alizarin complexone experiments. Fisheries Research 90, 271–278. https://doi.org/10.1016/j.fishres.2007.10.021

519 Flombaum, P., Gallegos, J.L., Gordillo, R.A., Rincón, J., Zabala, L.L., Jiao, N., Karl, D.M., Li,
520 W.K.W., Lomas, M.W., Veneziano, D., Vera, C.S., Vrugt, J.A., Martiny, A.C., 2013.
521 Present and future global distributions of the marine Cyanobacteria *Prochlorococcus* and
522 *Synechococcus*. PNAS 110, 9824–9829. https://doi.org/10.1073/pnas.1307701110
523 Fortier, L., Harris, R., 1989. Optimal foraging and density-dependent competition in marine fish
524 larvae. Marine Ecology Progress Series 51, 19–33. https://doi.org/10.3354/meps051019
525 Gelman, A., Hill, J., 2007. Data analysis using regression and multilevel/hierarchical models.
526 Cambridge University Press, New York.
527 Geoffroy, M., Bouchard, C., Flores, H., Robert, D., Gjøsæter, H., Hoover, C., Hop, H., Hussey,
528 N.E., Nahrgang, J., Steiner, N., Bender, M., Berge, J., Castellani, G., Chernova, N.,
529 Copeman, L., David, C.L., Deary, A., Divoky, G., Dolgov, A.V., Duffy-Anderson, J.,
530 Dupont, N., Durant, J.M., Elliott, K., Gauthier, S., Goldstein, E.D., Gradinger, R.,
531 Hedges, K., Herbig, J., Laurel, B., Loseto, L., Maes, S., Mark, F.C., Mosbech, A., Pedro,
532 S., Pettitt-Wade, H., Prokopchuk, I., Renaud, P.E., Schembri, S., Vestfals, C., Walkusz,
533 W., 2023. The circumpolar impacts of climate change and anthropogenic stressors on
534 Arctic cod (*Boreogadus saida*) and its ecosystem. Elementa: Science of the
535 Anthropocene 11, 00097. https://doi.org/10.1525/elementa.2022.00097
536 Geoffroy, M., Majewski, A., LeBlanc, M., Gauthier, S., Walkusz, W., Reist, J.D., Fortier, L.,
537 2016. Vertical segregation of age-0 and age-1+ polar cod (*Boreogadus saida*) over the
538 annual cycle in the Canadian Beaufort Sea. Polar Biology 39, 1023–1037.
539 https://doi.org/10.1007/s00300-015-1811-z
540 Goldstein, E.D., McCabe, R.M., Rogers, M.C., Deary, A.L., Duffy-Anderson, J.T., 2023. Loss of
541 sea ice and intermittent winds alter distributions and diet resources of young forage fish
542 in the Chukchi sea. Progress in Oceanography 217, 103097.
543 https://doi.org/10.1016/j.pocean.2023.103097
544 Gomes, D.G.E., 2022. Should I use fixed effects or random effects when I have fewer than five
545 levels of a grouping factor in a mixed-effects model? PeerJ 10, e12794.
546 https://doi.org/10.7717/peerj.12794

547 Heintz, R.A., Vollenweider, J.J., 2010. Influence of size on the sources of energy consumed by
548 overwintering walleye pollock (*Theragra chalcogramma*). Journal of Experimental
549 Marine Biology and Ecology 393, 43–50. https://doi.org/10.1016/j.jembe.2010.06.030
550 Hop, H., Gjøsæter, H., 2013. Polar cod (*Boreogadus saida*) and capelin (*Mallotus villosus*) as
551 key species in marine food webs of the Arctic and the Barents Sea. Marine Biology
552 Research 9, 878–894. https://doi.org/10.1080/17451000.2013.775458
553 Hop, H., Tonn, W.M., 1998. Gastric evacuation rates and daily rations of Arctic cod
554 (*Boreogadus saida*) at low temperatures. Polar Biology 19, 293–301.
555 https://doi.org/10.1007/s003000050249
556 Kimmel, D.G., Eisner, L.B., Pinchuk, A.I., 2023. The northern Bering Sea zooplankton
557 community response to variability in sea ice: evidence from a series of warm and cold
558 periods. Marine Ecology Progress Series 705, 21–42. https://doi.org/10.3354/meps14237
559 Koenker, B.L., Laurel, B.J., Copeman, L.A., Ciannelli, L., 2018. Effects of temperature and food
560 availability on the survival and growth of larval Arctic cod (*Boreogadus saida*) and
561 walleye pollock (*Gadus chalcogrammus*). ICES Journal of Marine Science 75, 2386–
562 2402. https://doi.org/10.1093/icesjms/fsy062
563 Kohlbach, D., Graeve, M., A. Lange, B., David, C., Peeken, I., Flores, H., 2016. The importance
564 of ice algae-produced carbon in the central Arctic Ocean ecosystem: Food web
565 relationships revealed by lipid and stable isotope analyses. Limnology and Oceanography
566 61, 2027–2044. https://doi.org/10.1002/lno.10351
567 Kohlbach, D., Hop, H., Wold, A., Schmidt, K., Smik, L., Belt, S.T., Woll, M., Graeve, M.,
568 Goraguer, L., Foss, Ø., Assmy, P., 2024. Ice algae as supplementary food rather than
569 major energy source for the Barents sea zooplankton community. Progress in
570 Oceanography 229, 103368. https://doi.org/10.1016/j.pocean.2024.103368
571 Kohlbach, D., Schaafsma, F.L., Graeve, M., Lebreton, B., Lange, B.A., David, C., Vortkamp,
572 M., Flores, H., 2017. Strong linkage of polar cod (*Boreogadus saida*) to sea ice algae-
573 produced carbon: Evidence from stomach content, fatty acid and stable isotope analyses.
574 Progress in Oceanography 152, 62–74. https://doi.org/10.1016/j.pocean.2017.02.003
575 Kono, Y., Sasaki, H., Kurihara, Y., Fujiwara, A., Yamamoto, J., Sakurai, Y., 2016. Distribution
576 pattern of Polar cod (*Boreogadus saida*) larvae and larval fish assemblages in relation to

oceanographic parameters in the northern Bering Sea and Chukchi Sea. Polar Biology 39, 1039–1048. https://doi.org/10.1007/s00300-016-1961-7

Larsen, T., Ventura, M., Andersen, N., O'Brien, D.M., Piatkowski, U., McCarthy, M.D., 2013. Tracing carbon sources through aquatic and terrestrial food webs using amino acid stable isotope fingerprinting. PLoS ONE 8, e73441. https://doi.org/10.1371/journal.pone.0073441

Laurel, B.J., Spencer, M., Iseri, P., Copeman, L.A., 2016. Temperature-dependent growth and behavior of juvenile Arctic cod (*Boreogadus saida*) and co-occurring North Pacific gadids. Polar Biology 39, 1127–1135. https://doi.org/10.1007/s00300-015-1761-5

Lee, Y., Min, J.-O., Yang, E.J., Cho, K.-H., Jung, J., Park, J., Moon, J.K., Kang, S.-H., 2019. Influence of sea ice concentration on phytoplankton community structure in the Chukchi and East Siberian Seas, Pacific Arctic Ocean. Deep Sea Research Part I: Oceanographic Research Papers 147, 54–64. https://doi.org/10.1016/j.dsr.2019.04.001

Legendre, P., and Gallagher, E. (2001). Ecologically meaningful transformations for ordination of species data. Oecologia 129, 271–280. doi: 10.1007/s004420100716

Legendre, P., Legendre, L., 2012. Numerical ecology. Elsevier, Amsterdam; The Netherlands.

Leu, E., Søreide, J.E., Hessen, D.O., Falk-Petersen, S., Berge, J., 2011. Consequences of changing sea-ice cover for primary and secondary producers in the European Arctic shelf seas: Timing, quantity, and quality. Progress in Oceanography 90, 18–32. https://doi.org/10.1016/j.pocean.2011.02.004

Levine, R.M., De Robertis, A., Grunbaum, D., Wildes, S., Farley, E.V., Stabeno, P.J., Wilson, C.D., 2023. Climate-driven shifts in pelagic fish distributions in a rapidly changing Pacific Arctic. Deep Sea Research Part II: Topical Studies in Oceanography 208, 105244. https://doi.org/10.1016/j.dsr2.2022.105244

Lin, P., Pickart, R.S., McRaven, L.T., Arrigo, K.R., Bahr, F., Lowry, K.E., Stockwell, D.A., Mordy, C.W., 2019. Water mass evolution and circulation of the northeastern Chukchi Sea in summer: Implications for nutrient distributions. Journal of Geophysical Research Oceans 124, 4416–4432. https://doi.org/10.1029/2019JC015185

Llopiz, J., Cowen, R., 2009. Variability in the trophic role of coral reef fish larvae in the oceanic plankton. Marine Ecology Progress Series 381, 259–272. https://doi.org/10.3354/meps07957

608 Marsh, J.M., Mueter, F.J., Quinn, T.J., 2020. Environmental and biological influences on the
609 distribution and population dynamics of polar cod (*Boreogadus saida*) in the US Chukchi
610 Sea. Polar Biology 43, 1055–1072. https://doi.org/10.1007/s00300-019-02561-w
611 Matarese, A.C., Blood, D.M., Picquelle, S.J., Benson, J.L., 2003. Atlas of abundance and
612 distribution patterns of ichthyoplankton from the Northeast Pacific Ocean and Bering Sea
613 ecosystems: based on research conducted by the Alaska Fisheries Science Center (1972–
614 1996) [WWW Document]. URL http://spo.nwr.noaa.gov/pp1.pdf (accessed 12.29.16).
615 Mazur, M.M., Wilson, M.T., Dougherty, A.B., Buchheister, A., Beauchamp, D.A., 2007.
616 Temperature and prey quality effects on growth of juvenile walleye pollock *Theragra*
617 *chalcogramma* (Pallas): a spatially explicit bioenergetics approach. Journal of Fish
618 Biology 70, 816–836. https://doi.org/10.1111/j.1095-8649.2007.01344.x
619 Meekan, M.G., Carleton, J.H., McKinnon, A.D., Flynn, K., Furnas, M., 2003. What determines
620 the growth of tropical reef fish larvae in the plankton: food or temperature? Marine
621 Ecology Progress Series 256, 193–204.
622 Methot, R.D., 1986. Frame trawl for sampling pelagic juvenile fish. California Cooperative
623 Oceanic Fisheries Investigations Reports 27: 267-278
624 Mueter, F.J., Nahrgang, J., Nelson, R.J., Berge, J., 2016. The ecology of gadid fishes in the
625 circumpolar Arctic with a special emphasis on the polar cod (*Boreogadus saida*). Polar
626 Biology 39, 961–967. https://doi.org/10.1007/s00300-016-1965-3
627 Oberpriller, J., de Souza Leite, M., Pichler, M., 2022. Fixed or random? On the reliability of
628 mixed-effects models for a small number of levels in grouping variables. Ecology and
629 Evolution 12, e9062. https://doi.org/10.1002/ece3.9062
630 Ogle, D.H., Doll, J.C., Wheeler, A.P., Dinno, A., 2025. FSA: Simple Fisheries Stock Assessment
631 Methods. doi:10.32614/CRAN.package.FSA, R package version 0.10.0, https://CRAN.R-
632 project.org/package=FSA
633 Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R.,
634 Solymos, P., Stevens, M., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B.,
635 Borcard, D., Borman, T., Carvalho, G., Chirico, M., De Caceres, M., Durand, S.,
636 Evangelista, H., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M., Lahti,
637 L., McGlinn, D., Ouellette, M., Ribeiro, C.E, Smith, T., Stier, A., Ter Braak, C., Weedon,

638 J,. 2025. vegan: Community Ecology Package. R package version 2.7-0,
639 https://vegandevs.github.io/vegan/.
640 Pedersen, E.J., Miller, D.L., Simpson, G.L., Ross, N., 2019. Hierarchical generalized additive
641 models in ecology: an introduction with mgcv. PeerJ 7, e6876.
642 https://doi.org/10.7717/peerj.6876
643 Questel, J.M., Blanco-Bercial, L., Hopcroft, R.R., Bucklin, A., 2016. Phylogeography and
644 connectivity of the *Pseudocalanus* (Copepoda: Calanoida) species complex in the eastern
645 North Pacific and the Pacific Arctic Region. Journal of Plankton Research 38, 610–623.
646 https://doi.org/10.1093/plankt/fbw025
647 R Core Team (2024). R: A Language and Environment for Statistical Computing. R Foundation
648 for Statistical Computing, Vienna, Austria. https://www.R-project.org/
649 Randall, J.R., Busby, M.S., Spear, A.H., Mier, K.L., 2019. Spatial and temporal variation of late
650 summer ichthyoplankton assemblage structure in the eastern Chukchi Sea: 2010–2015.
651 Polar Biology 42, 1811–1824. https://doi.org/10.1007/s00300-019-02555-8
652 Robert, D., Shoji, J., Sirois, P., Takasuka, A., Catalán, I.A., Folkvord, A., Ludsin, S.A., Peck,
653 M.A., Sponaugle, S., Ayón, P.M., Brodeur, R.D., Campbell, E.Y., D'Alessandro, E.K.,
654 Dower, J.F., Fortier, L., García, A.G., Huebert, K.B., Hufnagl, M., Ito, S., Joh, M.,
655 Juanes, F., Nyuji, M., Oozeki, Y., Plaza, G., Takahashi, M., Tanaka, Y., Tojo, N., Watari,
656 S., Yasue, N., Pepin, P., 2023. Life in the fast lane: Revisiting the fast growth—High
657 survival paradigm during the early life stages of fishes. Fish and Fisheries 24, 863–888.
658 https://doi.org/10.1111/faf.12774
659 Sherr, E.B., Sherr, B.F., Hartz, A.J., 2009. Microzooplankton grazing impact in the Western
660 Arctic Ocean. Deep Sea Research Part II: Topical Studies in Oceanography 56, 1264–
661 1273. https://doi.org/10.1016/j.dsr2.2008.10.036
662 Sogard, S.M., 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review.
663 Bulletin of Marine Science 60, 1129–1157
664 Sokal, R.R. and Rohlf, F.J. (1995) Biometry: The Principles and Practice of Statistics in
665 Biological Research. 3rd Edition, W.H. Freeman and Co., New York.
666 Søreide, J.E., Leu, E., Berge, J., Graeve, M., Falk-Petersen, S., 2010. Timing of blooms, algal
667 food quality and *Calanus glacialis* reproduction and growth in a changing Arctic. Global
668 Change Biology 16, 3154–3163. https://doi.org/10.1111/j.1365-2486.2010.02175.x

669 Spear, A., Napp, J., Ferm, N., Kimmel, D., 2020. Advection and in situ processes as drivers of
670 change for the abundance of large zooplankton taxa in the Chukchi Sea. Deep Sea
671 Research Part II: Topical Studies in Oceanography, Understanding Ecosystem Processes
672 in the Pacific Arctic 177, 104814. https://doi.org/10.1016/j.dsr2.2020.104814
673 Sponaugle, S., 2009. Gathering information from otoliths of tropical fishes. Springer, pp. 93–
674 132.
675 Sreenivasan, A., Heintz, R., 2016. Estimation of the relationship between growth, consumption,
676 and energy allocation in juvenile pacific cod (*Gadus macrocephalus)* as a function of
677 temperature and ration. Deep Sea Research Part II: Topical Studies in Oceanography 132,
678 154–161. https://doi.org/10.1016/j.dsr2.2016.04.004
679 Stabeno, P., Bell, S., Berchok, C., Cokelet, E., Cross, J., McCabe, R., Mordy, C., Overland, J.,
680 Strausz, D., Sullivan, M., Tabisola, H., 2023. Long-term biophysical observations and
681 climate impacts in US Arctic marine ecosystems. Oceanography 36(2-3): 78-85.
682 https://doi.org/10.5670/oceanog.2023.225
683 Strasburger, W.W., Hillgruber, N., Pinchuk, A.I., Mueter, F.J., 2014. Feeding ecology of age-0
684 walleye pollock (*Gadus chalcogrammus*) and Pacific cod (*Gadus macrocephalus*) in the
685 southeastern Bering Sea. Deep Sea Research Part II: Topical Studies in Oceanography,
686 Understanding Ecosystem Processes in the Eastern Bering Sea III 109, 172–180.
687 https://doi.org/10.1016/j.dsr2.2013.10.007
688 Venables, W.N., Ripley, B.D., 2002 Modern Applied Statistics with S. Fourth Edition. Springer,
689 New York. ISBN 0-387-95457-0
690 Vestfals, C.D., Mueter, F.J., Hedstrom, K.S., Laurel, B.J., Petrik, C.M., Duffy-Anderson, J.T.,
691 Danielson, S.L., 2021. Modeling the dispersal of polar cod (*Boreogadus saida*) and
692 saffron cod (*Eleginus gracilis*) early life stages in the Pacific Arctic using a biophysical
693 transport model. Progress in Oceanography 196, 102571.
694 https://doi.org/10.1016/j.pocean.2021.102571
695 Weingartner, T., Dobbins, E., Danielson, S., Winsor, P., Potter, R., Statscewich, H., 2013.
696 Hydrographic variability over the northeastern Chukchi Sea shelf in summer-fall 2008–
697 2010. Continental Shelf Research 67, 5–22. https://doi.org/10.1016/j.csr.2013.03.012

698 Welch, H.E., Bergmann, M., Siferd, T., Martin, K., Curtis, M., Crawford, R., Conover, R., Hop,
699 H., 1992. Energy flow through the marine ecosystem of the Lancaster Sound region,
700 Arctic Canada. Arctic 45, 342–357.
701 Wood, S.N., 2017. Generalized additive models: an introduction with R, Second edition. ed,
702 Chapman & Hall/CRC texts in statistical science. CRC Press/Taylor & Francis Group,
703 Boca Raton
704 Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed effects models
705 and extensions in ecology with R, Statistics for biology and health. Springer, New York,
706 NY.

Tables

Table 1. Generalized additive models (GAMs) linking recent growth (average otolith increment width for the most recent 5 days prior to capture, µm/day) with intrinsic factors, environmental factors, and diet from gut content analysis (diet). Model description identifies whether the full model included diet information, references the model equation [Equation 1 (Eq 1) or Equation 2 Eq 2)], and provides additional model descriptions. Rank identifies the top two models (selected model in bold) for each model description category. Two alternative (alt) models are also presented to confirm that patterns were consistent among relevant subsets of the data: fish from 2017 and 2018 only (no 2019) and diet fish only. Model lists the smooth terms [s()] and parametric terms in each model. $PC1_{diet}$ and $PC3_{diet}$ are PCA axis 1 and 3 scores from the diet PCA analysis (see Fig. 3). $Growth_{early}$ is otolith radius from the first 10 days of life. T_{20} and S_{200} are average temperature from the surface to a depth of 20 m and average salinity to a depth of 200 m, respectively. Adjusted coefficient of determination (R^2), Akaike information criterion adjusted for small sample sizes (AICc), and sample size (N) are shown for all models. AIC is not provided for the Diet (Eq 1): no 2019 model since the sample subset differs from all other models presented. See Supplemental Table 3 for additional model comparisons.

Model description	Rank	Model	R^2	AICc	N
Diet (Eq 1)	**1**	**$s(PC1_{diet}) + s(PC3_{diet})$**	**0.43**	**35.81**	**51**
	2	$s(PC1_{diet}) + s(PC3_{diet}) + Growth_{early}$	0.45	35.10	51
No diet (Eq 2)	**1**	**T_{20}**	**0.06**	**69.57**	**72**
	2	$S_{200} + T_{20}$	0.07	70.12	72
Diet (Eq 1): no 2019	alt	$s(PC1_{diet}) + s(PC3_{diet})$	0.30	-	41
No diet (Eq 2): diet fish only	alt	T_{20}	0.13	52.61	51

Figure Captions

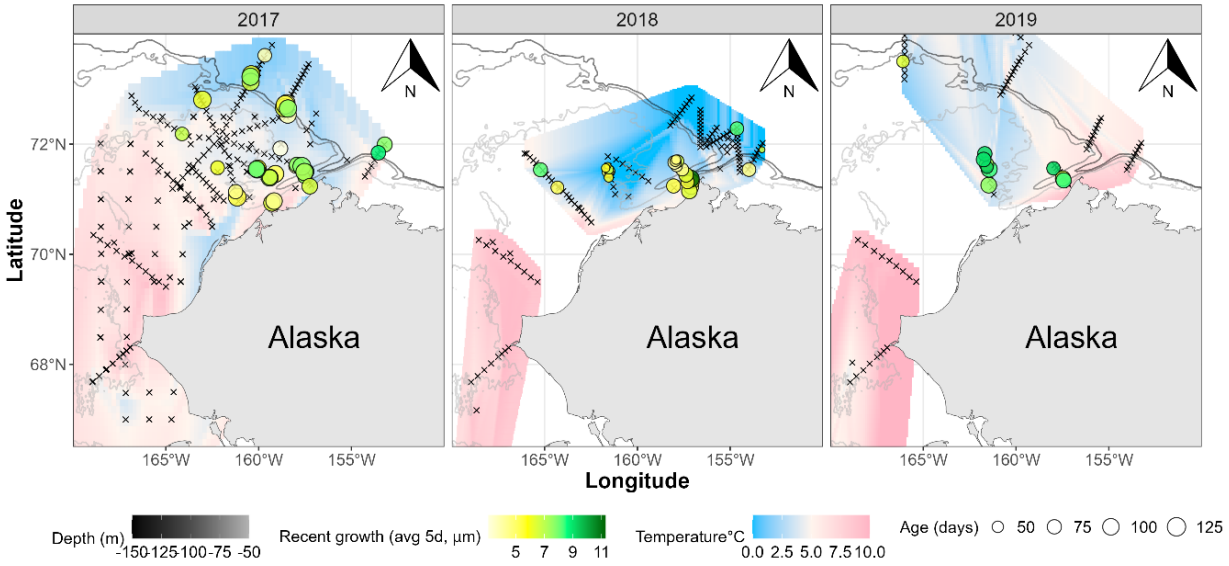
Figure 1. Polar cod (*Boreogadus saida*) catch locations in the Chukchi Sea from three years (2017-2019; circle symbols) and interpolated co-collected CTD temperature data from the same surveys averaged over the top 20 m of the water column ("x" symbols show station locations) to correspond with generalized additive model results (Table 1; see Supplemental Fig. 1 for average temperature over the top 200 m). The color scale for fish catch locations shows average otolith-derived growth (µm/day) for the most recent 5 days of life preceding capture. The size of circles indicates otolith-derived age of each sample and circles are jittered to minimize overlap.

Figure 2. Otolith-derived hatch and growth information for polar cod by year. (A) Kernel density distribution of hatch day of year where *n* is sample size (see Supplemental Table 1). (B) Age versus length where line fits are a Gompertz function (solid; root mean square error=3.79; Ogle et al., 2025) and a linear fit (dotted; root mean square error=3.94). (C) Otolith radius from the otolith core through the first 10 days of life (early growth). Boxplots show the median (line), the 1st and 3rd quartiles (hinges), and upper and lower whiskers that extend from the hinge to the largest (upper) and smallest (lower) value no further than 1.5 times the inter-quartile range, and outliers beyond the whiskers (points). (D) Mean growth (±SD) measured from the first full day prior to capture (day 1) until increments were no longer interpretable at the otolith edge focal plane. The dark gray line delineates the first 10 days prior to capture. The light gray line (15 days) shows the 1st quartile of increments measured from the edge. (E) Mean otolith increment width (±SD) by back-calculated age. Age was back-calculated using catch date, fish age, and increment count from the otolith edge. Back-calculated ages are averaged for ages with at least 3 observations and exclude increment widths greater than 15 days prior to capture (e.g., 1st quartile) since few specimens had measurements beyond that window of time.

Figure 3. Principal component (PC) analysis of gut content diet data from larval and juvenile polar cod (*Boreogadus saida*) showing PC axes 1 and 2 (A, B) and PC axes 3 and 4 (C, D). (A) and (C) show specimen scores (scaled to preserve Euclidean distance between points) color coded by year. (B) and (D) show vector loadings (bold arrows) with labels that describe the copepod prey taxa (scaled to ensure that angles between vectors reflect their correlations). To aid in interpretation, dotted line segments connect offset labels with corresponding vectors loadings. Symbol size in (A) and (C) corresponds to fish standard length (mm). The color scale in (B) and (D) shows interpolated temperature data averaged throughout the water column from each catch location to visualize temperature associations of prey items (interpolations correspond to points in A and C but are scaled to correspond with B and D). Percentages refer to the amount of variability in the data described by each PC axis. Abbreviated taxa include taxonomic descriptions where the prefix "C_" designates copepods. Abbreviations are provided in Supplemental Table 2.

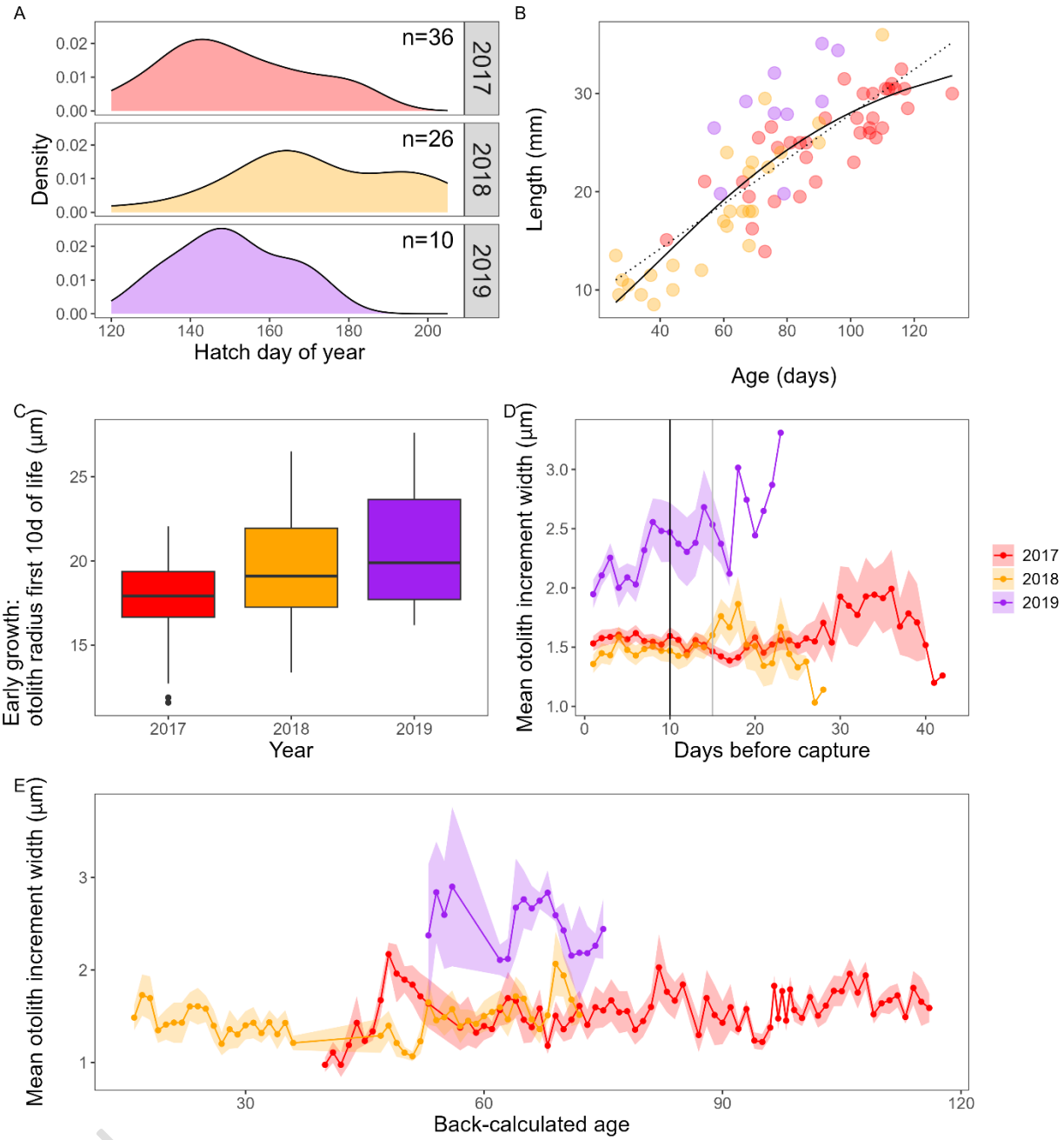
Figure 4. (A) Linear Discriminant Analysis (LDA), adapted from Goldstein et al. (2023) to visualize relationships between compound-specific stable isotopes of amino acids (CSIA-AA $\delta^{13}C$) from polar cod tissue, sea-ice particulate organic matter (iPOM), pelagic particular organic matter (pPOM), and potential carbon sources used to develop the LDA [Microalgae, *Synechococcus* spp. (Syn) combined with Dinoflagellates (Dino), and bacteria]. CSIA-AA $\delta^{13}C$ from polar cod, iPOM, and pPOM are predictions (solid symbols) and polar cod specimens (labeled 2017 and 2018) are color coded by collection year. (B) Redundancy analysis triplot showing the influence of polar cod diet composition (PC scores 1-3 shown in Fig. 3) on CSIA-AA $\delta^{13}C$. Points are polar cod specimens and symbol size corresponds with fish age. Black vectors are explanatory variables. Gray vectors are response variables where angles between vectors approximate their linear correlations. In (A) and (B) essential amino acids from CSIA-AA $\delta^{13}C$ used for analyses are abbreviated as Val (Valine), Leu (Leucine), and Ile (Isoleucine).

Figure 5. Generalized additive model partial effects plots [Table 1: Diet (Eq 1) selected model] showing relationships between otolith-derived recent growth (µm/day; increment widths averaged over 5 days prior to capture) and A) PC1 diet scores and B) PC3 diet scores. Smooth terms are denoted by s() and gray bands are 2 standard errors above and below the estimates of the terms.



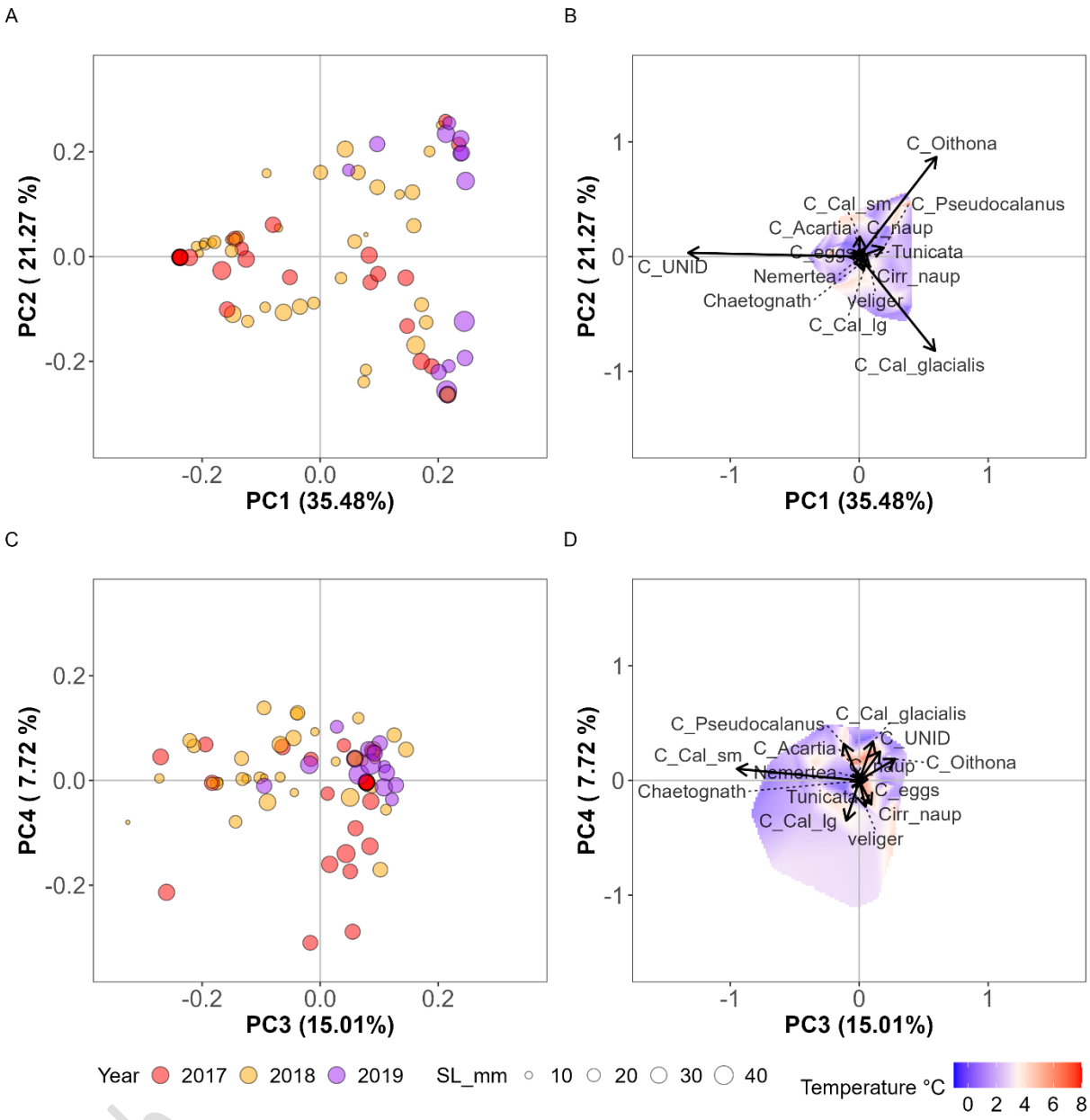
783

784 **Figure 1.**



785

786 **Figure 2.**



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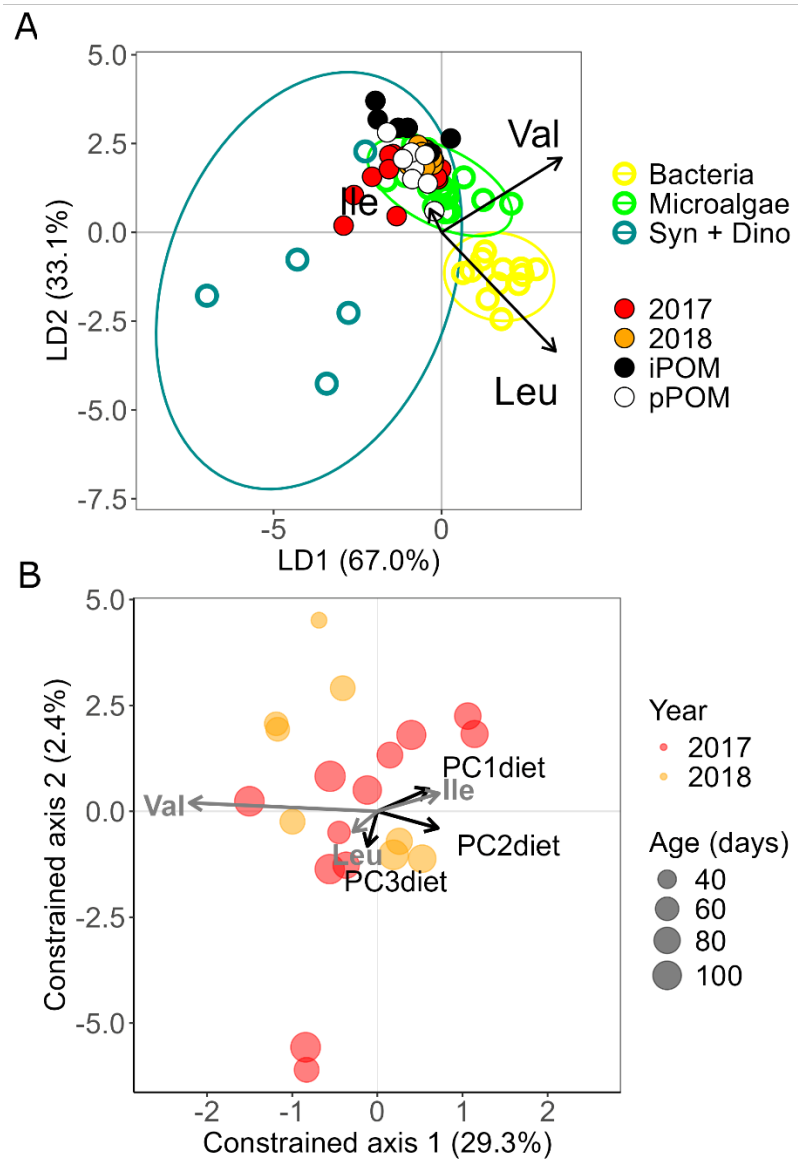
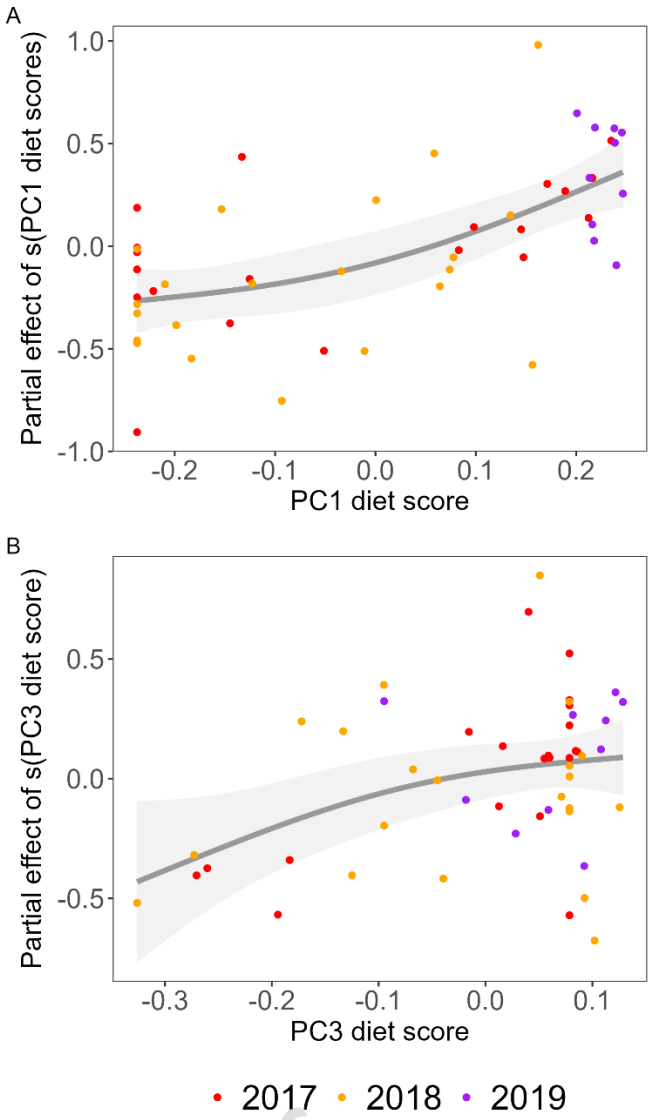
788 **Figure 3.**



789

790 **Figure 4.**



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792 **Figure 5.**